# A Complex Systems Approach to an Interpretation of Dynamic Brain Activity I: Chaotic itinerancy can provide a mathematical basis for information processing in cortical transitory and nonstationary dynamics

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**Abstract.** The transitory activity of neuron assemblies has been observed in various areas of animal and human brains. We here highlight some typical transitory dynamics observed in laboratory experiments and provide a dynamical systems interpretation of such behaviors. Using the information theory of chaos, it is shown that a certain type of chaos is capable of dynamically maintaining the input information rather than destroying it. Taking account of the fact that the brain works in a noisy environment, the hypothesis can be proposed that chaos exhibiting noise-induced order is appropriate for the representation of the dynamics concerned. The transitory dynamics typically observed in the brain seems to appear in high-dimensional systems. A new dynamical systems interpretation for the cortical dynamics is reviewed, cast in terms of high-dimensional transitory dynamics. This interpretation differs from the conventional one, which is usually cast in terms of low-dimensional attractors. We focus our attention on, in particular, chaotic itinerancy, a dynamic concept describing transitory dynamics among "exotic attractors", or "attractor ruins". We also emphasize the functional significance of chaotic itinerancy.

## 1 The background of lecture I

Cortical activity appears to be unstable. A single time series of such activity is often observed to be "nonstationary" with aperiodic changes between synchronized and desynchronized states, transitory dynamics between quasi-attractors ("attractor ruins" in our words), propagation of activity with various frequencies and the appearance and disappearance of phase-related synchronizations. Based on model studies, we propose the hypothesis that chaotic itinerancy can be universally observed not only in cortical synaptic networks but also in cortical gap junction systems, though in the latter it appears in a different way.

Before proceeding to the main issue, let us raise a naive but fundamental question concerning brain function. What is the brain doing? There can, of course, be various possible answers, but probably the most fundamental one would be that it is interpreting signals, not only those arising from the external world, but also those created within itself. The reason is the following. The purpose of cognition may be to discover the nature of objects. The purpose of movement may be to influence the rule of behavior, as well as to achieve cognitive purpose. If complete information is provided in advance of these processes, then the brain can uniquely solve the problem concerned and does not need interpretation. Usually, however, the information that the brain receive is only incomplete one. Therefore, the brain must interpret the information and determine its nature. This consideration leads us to the study of hermeneutics of the brain [1–6].

What kind of level of activity should be considered ? The dynamic features of the brain might mainly appear in its activity at the mesoscopic level. At the microscopic level, that is, at single channel or single neuron levels, the brain activity appears to be highly irregular and nonstationary. On the other hand, at the macroscopic level, that is, at the level of a functional area or of the whole brain, the activity appears to be much less disordered. According to a conventional theory of phase transitions developed in physics, a macroscopic ordered motion can appear as the result of cooperativity of microscopic elements of the system concerned. The ordered motion can be described by one or more order parameters. In equilibrium phase transitions, two thermal equilibrium states are interchanged by changes in a control parameter such as temperature, magnetic field, etc. In a neighborhood of the critical point of the transition, complex nonequilibrium motions appear. The characteristic scales in space of the system in such a critical regime range from microscopic to macroscopic. Then, the time-dependent phenomena can be observed at the mesoscopic level, and such a temporal evolution indicates the appearance of ordered motions.

A similar situation can also occur in far-from-equilibrium systems, where in place of thermal equilibrium states various kinds of nonequilibrium stationary states can form the basis of phenomena. The state transitions in far-from-equilibrium systems can be described by bifurcations. We here apply this framework to the transitions that appear during the dynamic brain activity. The term "critical point" is replaced by the term "bifurcation point" within this framework. Dissipative systems are typical far-from-equilibrium systems, where a stationary inflow and outflow of energy or matter plays a role in maintaining the stationary state. In such a system, order parameters often behave time-dependently. Thus, the motions can be described by the time-dependency of quantities such as density functions, where a density function is, in general, a function of space, time and other quntities such as the membrane potential of neurons and the calcium concentrations inside the membrane, namely $\rho(x, s, t) = \rho(x, (v, c), t)$. Thus, it is called a mesoscopic-level description. A typical equation of motion at this level is the Navier-Stokes equation of hydrodynamics. The description of complex spatio-temporal patterns in the brain must be made at the mesoscopic level.

A further crucial problem stems from the fact that the brain works in a noisy environment. Its mechanism has not yet been clarified. In this situation, we assume that the interplay between noise and dynamical systems provides clue for solving the problem of how the brain treats noisy signals. Among others, noise-induced order [32], stochastic resonance [8], and chaotic resonance [9] are noteworthy. Noise-induced order occurs in a certain class of chaotic dynamical systems. At a particular noise level, a transition appears from the chaotic state to the ordered state, characterized by the appearance of sharp peak in the power spectrum, an abrupt decrease of Kolmogorov-Sinai entropy, and a change of the Lyapunov exponent from positive to negative values. The orbit is aggregated rather than segregated by the noise. In multi-stable systems, the most stable state is usually selected by adding noise, provided that the noise itself does not destabilize the stable states. If external noise is superimposed upon a periodic force, the state may change to resonate the periodic force. This is termed a stochastic resonance. A similar resonance may occur in the chaotic environment, where chaos replaces noise. This is called a chaotic resonance. This idea was suggested, based on the observations that both chaos and noise are ubiquitous in the brain.

Curious transitory phenomena have been observed in various conditions in animal and even human brains. Among others, the typical phenomena appear as chaotic transitions between quasi-attractors [10–13], "nonstationary" alteration between synchronized and desynchronized states [14], the propagation of wave packets of $\gamma$- and $\delta$- range activity [15, 16], and the synchronization of epochs with large phase differences that appear irregularly [17]. These curious phenomena possess the common feature that the autonomic transition between states is both chaotic and itinerant. These states can be described by a conventional attractor. Actually, there have been a number of interpretation of brain activity in terms of the attractor concept. However, a conventional attractor, that is, a geometric attractor, is an inappropriate model for the interpretation of these transitory dynamics. Because the transitory dynamics appear to be transition between states, such a state should be described as unstable. Thus, we must find a new model for such a state, in other words, we must introduce a new model for the dynamic process such that it allows for both stability and instability. Here, instability describes a transition from such a state, and stability describes the return to the original state. We must extend this process further to successive transitions between multiple states. We have proposed *chaotic itinerancy* as a most appropriate concept for such transitory dynamics [18–20, 3, 4].

For further details of the background of this study, in particular, for the significance of the interpretation of brain dynamics in terms of high-dimensional dynamical systems and also for the potential role of chaotic itinerancy, the readers can refer to the recent magnum opus [4] of one of the authors (IT). The references on complex systems (see, for example, the reference [22]) are also highly recommended.

## 2 Theoretical basis for the interpretation of cortical dynamic activity

There seems to be a common mechanism underlying all the dynamic behaviors described above. To study such an underlying mechanism, chaotic dynamical systems of high dimension and the information theory of chaotic dynamical systems are required.

### 2.1 Attractors

We would like to describe the dynamic activity mentioned above in terms of the concepts of dynamical systems. Cortical dynamic behavior appears to be based on far-from-equilibrium states. To maintain a system in such a state, a continuous energy pumping is necessary, because of the energy dissipation that is inevitable in all living systems. Thus, it is natural to use the attractor concept.

Let us, therefore, consider the relationship between a kind of attractor and a dynamic state. Stationary or steady states in behavior can be represented by a fixed point, namely a point attractor. Furthermore, periodic, quasi-periodic and irregular motions can be represented by a limit cycle, a torus and a strange attractor, respectively. It should be noted that the term, 'strange attractor' was proposed [23] as the name for the fourth attractor following a fixed point, a limit cycle and a torus, indicating a turbulent state expected to appear after the collapse of tori of three and higher dimension by the infinitesimal interactions between variables. Hence, rigorously speaking, the use of this concept should be restricted to descriptions of attractors that appear after the collapse of tori of finite dimension, where such finite dimensionality is precisely the difference between this theory and Landau theory of hydrodynamic turbulence. In this respect, the strange attractor can be distinguished from ordinary chaotic attractors for which different scenarios from the one by successive Hopf bifurcations are provided, such as successive period doubling bifurcations or saddle-node bifurcations. In recent literature, however, the term, 'strange attractor' has been used to describe all chaotic attractors. In the present article, we follow this conventional use of the terminology, but have restricted it to relatively low-dimensional chaos.

These four kinds of attractors appear also in lower-dimensional dynamical systems, up to three dimensions. At least three dimensions are necessary for the appearance of a strange attractor in the case of vector fields, whereas only one dimension is enough for the existence of chaos in a discrete map. Thus, *three* is a critical number for the presence of strange attractors.

Hyperchaos, proposed by Rössler [24], is defined as possessing plural positive Lyapunov exponents, giving rise to the number *four* as the critical dimensionality because of the presence of at least two dimensions for instability, at least one dimension for dissipation, i.e., for stability, and one orbital dimension. The concept of hyperchaos may be one of the key concepts for the dynamic description of the high-dimensional irregular activity of the brain. It is, however, insufficient for the dynamic concepts by which the transitory dynamics is adequately represented (in most cases appearing to be aperiodically itinerant), because hyperchaos does not distinguish between the itinerant transitory dynamics and simply chaotic dynamics. Our interest here is a common dynamic representation for such transitory dynamics observed in the brain. Thus, a high-dimensional dynamic description is necessary to interpret the transitory and itinerant processes. This description may provide a new key to modeling the dynamics of brain activity. We claim that *chaotic itinerancy* is an adequate dynamic description for such processes.

We can discuss the critical dimensionality of chaotic itinerancy. According to Kaneko [25], let us estimate two factors that are supposed to determine the dimensionality for the chaotic transition. Let $N$ be the system's dimension. Let us assume that the number of states in each dimension is two, taking into account the presence of two stable states separated by a saddle. The number of admissible orbits cyclically connecting the subspaces increases in proportion to $(N-1)!$, whereas the number of states increases in proportion to $2^N$. If the former number exceeds the latter, then all orbits cannot necessarily be assigned to each of the states, hence causing the transitions. In this situation, we expect itinerant motions between states. This critical number is *six* for chaotic itinerancy [25, 26]. This critical dimensionality may provide us with the boundary between low- and high-dimensional dynamical systems.

As discussed below, several scenarios describing the appearance of chaotic itinerancy can be considered, such as the typical case of the appearance of Milnor attractors [29]. A Milnor attractor is, by definition, accompanied with positive measure of the orbits attracted to it. It can also be accompanied by the orbits repelled from it. The lowest dimension of a Milnor attractor is a fixed point that appears in the critical situation of the tangent bifurcation in one-dimensional maps or the saddle-node bifurcation in higher dimensions [29, 31].

### 2.2 Information structure and noise effect

So far, we have classified the dynamical systems with the dimensionality of attractors, and also proposed the use of chaotic itinerancy to give a dynamic description for the transitory dynamics observed in the brain. Because the brain works in a noisy environment, however, one must consider the effects of noise on dynamical systems and the information processing of such noisy dynamical systems.

Other than stochastic resonance, which is now well known as the crucial effect of noise with periodic forcing, there can be several effects of noise in the presence of chaos. In the case of the presence of a complicated basin structure such as seen in, for example, the KIII model of Freeman, the system behaves so that the external noise enhances the chaotic response of the olfactory bulb that detects an odor [27, 28].

Furthermore, the existence of nonuniform chaos can be justified in excitable systems such as neural systems and such chaos possesses peculiar characteristics. The nonuniformity stems from the nonuniformity of the Markov partition, which provides the inherent scale of measure of the Markov states. Thus, this brings about uneven probabilities of the residence time of orbits to Markov states. This inherent scale of observation is mismatched with the scale given by external noise, for example, the uniform scale when uniform noise is applied. This mismatch plays a role in generating ordered motions out of chaos when noise is applied. This has been called noise-induced order [32].

This property of excitable systems has been claimed to be effective for the transmission of input information in chaotic systems [33–35]. For the first time, let us review information theory, which clarifies the information structure of low-dimensional chaotic systems, and then let us examine the propagation of input information in the coupled chaotic systems. Without loss of generality, let us consider a differentiable map $f$ defined on the interval $I$, $f : I \rightarrow I$. We consider the information contained in the initial conditions. Because one cannot assign the initial conditions with infinite precision, one must consider the distribution for the assignment of initial conditions. In the usual computer simulations, this assignment may be a uniform distribution, or it may be a Gaussian distribution in the case of the usual laboratory experiments. Or, one may consider from the beginning, a certain probability distribution as an initial distribution. Thus, we consider the information contained in the given distribution $p(x)$ and also its evolution according to the evolution of dynamical systems.

To see this, let us define the Kullback divergence which indicates the relative information content of $p(x)$ to $q(x)$:

$$I(p) = \int dxp(x)log\frac{p(x)}{q(x)}, \tag{1}$$

where $x \in I$. The evolution of the distribution is provided by the Frobenius-Perrone operator $F$, which is defined as follows:

$$Fp(x) = \sum_{f^{-1}(x)=y} \frac{p(y)}{|f'(y)|}, \tag{2}$$

where $f'(y)$ indicates the derivative of $f$ with respect to $y$, and the summation is taken over the inverse image of $x$.

Let us define the *information flow* by the difference between the Kullback divergence before and after applying the operation.

$$\Delta I(p) = I(p) - I(Fp). \tag{3}$$

We describe the evolution of information contained in the probability distribution relative to the stationary distribution $p^*(x)$ of the system. This $p^*(x)$ is invariant under the operator $F$, i.e., $Fp^*(x) = p^*(x)$. The following equation holds if $p^*(x)$ is absolutely continuous with respect to the Lebesgue measure, that is, if $p^*(x) \rightarrow 0$ as the Lebesgue measure $m(x)$ goes to zero.

$$\Delta I(p) = \int dxp^*(x)log|df(x)/dx|. \tag{4}$$

The right hand side of this equation is just the Lyapunov exponent. Therefore, the information flow is provided by the Lyapunov exponent. Oono [36] and

Shaw [37] gave essentially the same treatment. The above formulae, eq. (3) and eq. (4), show that the initial slope of the decay of information with respect to the evolution of the distribution by $F$ provides the Lyapunov exponent.

It is, however, not sufficient to reveal the details of the information structure. In chaotic systems, a local divergence rate fluctuates according to the distribution of derivatives (eigenvalues of Jacobian matrix in high-dimensional maps and also in vector fields), which gives rise to the fluctuations in information flow. Furthermore, our observation is limited to not only the highest digit, but also the lowest one, so that the observation is restricted to a finite window. By the Lyapunov exponent, only the information lost at (or flowing out of) the highest digit is calculated. We require another quantity by which all the information flowing out of the observation window is calculated. Such a quantity is mutual information.

$$I(i;j) = \sum_j p(j) log p(j)^{-1} - \sum_i \sum_j p(i) p(j/i) log p(j/i)^{-1}, \quad (5)$$

where $p(j/i)$ is a transition probability from state $i$ to state $j$. The mutual information is information shared between two states, thus one can calculate the information transmitted from one state to other states, and consequently one can obtain the detailed structure of the *fluctuations* of information flow.

By introducing a time-dependency into the definition of mutual information, we can further investigate *information mixing.*

$$I^{(n)}(i;j) = \sum_j p(j) log p(j)^{-1} - \sum_i \sum_j p(i) p^{(n)}(j/i) log p^{(n)}(j/i)^{-1}, \quad (6)$$

where $n$ is a time and $p^{(n)}(j/i)$ the transition probability from $i$ to $j$ after $n$ time-steps. There are typically two cases: (1) a linear decay of the mutual information in time and (2) an exponential decay, described as follows.

(1) $I(t) = I(0) - at$.

Taking the derivative with respect to $t$ on both sides, we obtain $dI(t)/dt = -a = const$. This implies that the same quantity of information decays in each time. This situation is the case that the fluctuation of information is very small, so that the information structure is adequately described by the Lyapunov exponent.

(2) $I(t) = I(0) exp(-rt)$

Taking the derivative with respect to $t$ on both sides, we obtain $dI(t)/dt = -rI(t)$, thus $(dI/dt)/I = -r = const$. This implies that the information quantity decays by the same ratio in each time. In this second situation, the fluctuation of information is large enough to produce the mixing property of information. The mixing property here means that each digit of the variable of dynamical system containes the information of any other digits. This is guaranteed by the calculations of bit-wise mutual information, because such calculations provide the shared information between any two digits.

The difference of properties between case (1) and case (2) demonstrates a crucial difference in the network properties of coupled chaotic systems, relating to the way input information is propagated and the dynamic maintenance of such information. The input information to such a network is dynamically maintained and is transmitted from one chaotic individual system to the others if each chaotic individual system possesses the large fluctuations of information flow as in case (2). Propagation of the input information can also be extended to other systems placed far from the input. On the other hand, if the network consists of chaotic systems that possess small fluctuations of information flow, as in case (1), then the network cannot have such properties.

One tends to think that chaos is useless for information processing, because input information appears to be destroyed by the orbital instability of chaos. The orbital instability rather brings about a role as *information source* [36, 37], because symbol sequences are produced by such orbital instability, provided that symbols and decision point(s) that determine the symbols are given. The evolution rule of states as a dynamic grammar determines a structure of admissible symbol sequences [38]. If the property of information mixing holds in each individual system, the input information can be dynamically maintained in its networks, in spite of the orbital instability of chaos, as mentioned above. Thus, chaotic networks of this kind can be considered to be an *information channel*.

The studies of chaos from the viewpoint of information processing have produced various ideas concerning the possibilities of the application of chaos to studies of the function of the brain and also to studies of the structure of mind. John Nicolis and others [39–42] proposed a great variety of discrimination of inputs by means of a chaotic system with multiple basins, especially in relation to a thalamo-cortical pathway for sensory information. Furthermore, the capacity of short-term memory (working memory), namely the magic number *seven plus or minus two* that G. Miller [43] found was estimated by means of chaotic dynamical systems. Recently, Kaneko has proposed another mechanism to generate this magic number with globally coupled map systems [25], which is related to the critical number, *six* for the appearance of chaotic itinerancy. Through the intensive and also extensive studies of animal olfaction, Freeman and his colleagues have clarified the dynamic mechanism of perception with chaos and chaotic itinerancy [11–13]. Taking into account the fact that the chaos produced in an excitable system (such as neurons and neuron assemblies) possesses the mixing property of information, it turns out that further large-scale networks can maintain information in a dynamic manner because of the presence of chaotic behavior. It should be noted that chaotic itinerancy also has the property of information mixing.

## 3 Chaotic itinerancy

In this section, we review the characteristics of chaotic itinerancy (CI) and also discuss possible mechanisms for the genesis of chaotic itinerancy.

### 3.1 Dynamic features of chaotic itinerancy

To show the dynamic features of CI, we here highlight two systems, both of which offer opportunities to study CI, together with another typical system [18]: one is a nonequilibrium neural network model for successive association of memories [44, 3] and the other is a globally coupled chaotic map [19]. In particular, it seems that these models show differences in mechanisms for the genesis of CI.

The neocortical architecture of neural networks has been studied in details. There is a common structure in different areas, while a specific one can be distinguished in each area. Although the relationship between structure and function is clearly one of the main problems in biological evolution and remains an open question, it seems likely that there is a strong correlation between them. From this point of view, we assume that a common functional feature for any information processing is manifested in the common network structure in all areas. We considered a dynamic phase of successive association of memories to represent such a functional feature. We adopted the network architecture described by Szentágothai [45–47] for our model.

The fundamental architecture of the model consists of the recurrent connections of the pyramidal cells and the feedback connections of interneurons, which provide randomly fixed positive or negative effects on the membrane potential depolarization of pyramidal cells. The effect of interneurons is provided by a model of the action of the spiny stellate cells and the basket cells. Such an architecture has been considered a fundamental modular element. The module in the model consists of two sub-modules and specific inhibitory neurons. The submodules are coupled to each other through weak connections from the pyramidal cells. Specific inhibitory neurons, which are considered to model the Martinocci cells or the double bouquet cells, make synaptic contact with the dendrites of the pyramidal cells in only one submodule.

The dynamics of the model were provided as a stochastic renewal with two types of neural dynamics: one is the stationary dynamics that maintain the neural state (to the previous state), and the other is the usual deterministic neural dynamics such as the integrate-and-fire model, though we used its discrete version in time. This stochastic dynamics was assumed to stem from the stochastic release of synaptic vesicles under the influence of inputs. Thus, this dynamics provides synaptic noise. We also introduced an additive noise in the model equation, considering function of dendritic noise.

The model simulations exhibited various crucial dynamic features that have been claimed to mimic fundamental functions associated with memory dynamics, such as successive transitions between stored memories, the reorganization of successive transitions after learning of new memories, the enhancement of memory capacity and the enhancement of accessibility to memory. The dynamic rule for the transitions, in particular, was chaotic, but critical. The skeleton of the rule can be described by a one-dimensional circle map, $f : I \rightarrow I, f(x) = x + asin(4\pi x) + c(mod 1), x \in I = [0, 1]$, at the critical phase such that the map makes a tangential contact with the diagonal line indicating the identity $f(x) = x$, where $x \in I$. For example, this occurs for $a \simeq 0.08$ when $c = 0.1$.

This critical situation often appears at the critical phase of intermittency that is realized just at the onset of tangent bifurcation in one-dimensional map, or saddle-node bifurcations in higher dimensional systems. This, however, does not hold in the present case. The neural network model we used is controlled by many parameters including various fixed coupling strengths and an updating rate of learning. The similar transitions that are characterized by dynamics possessing the same criticality as the case mentioned above are observed as changing the values of such parameters as long as the chaotic transition occurs. Therefore, we concluded [21] that this critical situation arises not from the bifurcation, but from the *self-organized criticality* [48]. We further claim that this critical situation is structurally stable because it remains even after changing the bifurcation parameters.

If cortical dynamics follow only deterministic dynamics such as the critical circle map, no transitions from such critical fixed points can occur because the critical fixed point $x^*$ derived from $x = f(x)$and $f'(x^*) = 1$ is a typical Milnor attractor [29], which is reached from a set of initial points with positive measure (but possessing unstable direction). The critical fixed points obtained represent stored memories or learned patterns, so no transitions between memories can occur in this situation. A little additive noise plays a role in triggering such transitions. Such a role for noise can be justified as a mechanism of CI. This issue will be discussed below.

CI can be characterized by several indices. Auto- and cross-correlations decay slowly, following the power law. Related to these quantities, time-dependent-mutual information follows an exponential decay or a power decay. Taking account of the dynamic storage of information in the network of nonuniform chaos, a macroscopic network consisting of the elemental networks that produce CI may retain input information. An $N$-dimensional dynamical system possesses an $N$-tuple of Lyapunov exponents, the 'Lyapunov spectrum', each of which indicates a long-time average of the eigenvalues of the products of the Jacobian matrices, where each Jacobian matrix describes a time evolution of the deviation of trajectories from a basal trajectory in a linear range, associated with the orthonormalization of state vectors. Thus, the indication of chaos, that is, the presence of orbital instability, is the existence of at least one positive Lyapunov exponent. In the presence of CI, the Lyapunov spectrum tends to include many near-zero exponents. Recently, two important reports were published on the Lyapunov exponents of CI. Sauer claims that the appearance of sustained fluctuations of the zero-Lyapunov exponent is a characteristic of CI [49]. Tsuda and Umemura claim that a further characteristic of CI is that even the largest Lyapunov exponent converges in an extremely slow way, associated with large fluctuations [31]. It should be noted that CI differ from simple chaotic transitions in the sense that in CI, stagnant motions at attractor ruins or near Milnor attractors appear. This is characterized by a probability distribution of residence time at attractor ruins: a power decay in the case of CI in the nonequilibrium neural network [21]. To explain these characteristics of CI, we considered the chaotic transitions between *attractor ruins* that are no longer attractors but can attract some orbits. The closest concept to attractor ruin is an attractor in Milnor's sense. For this reason, we have been interested in a Milnor attractor.

Before defining Milnor attractors, let us remember the conventional definition of an attractor, namely a geometric attractor. Let $M$ be a compact smooth manifold. Let $f : M \to M$ be a continuous map. We denote a geometric attractor by $A$. A subset $N$ of $M$ satisfying $f(N) \subset inter(N)$ is called a trapping region, where $inter(N)$ indicates an interior of $N$. The equation $A = \bigcap_{n=0}^{\infty} f^{(n)}(N)$ defines an attracting set. A geometric attractor is defined as a minimal attracting set, that is, it is an attracting set satisfying a topological transitivity. Thus any two points in a neighborhood of an attractor do not move far away from each other.

Milnor extended the definition of attractor [29, 50]. Let us define the attractor in Milnor's sense. Let $B$ be a Milnor attractor. Let $\rho(B)$ be a basin of $B$, which is defined as $\rho(B) = \{x|\omega(x) = B, x \in M\}$. Here $\omega(x)$ is an $\omega$-limit set of $x$. An $\omega$-limit set is a set of $\omega$-limit points, where an $\omega$-limit point of $x$ for $f$ is a point to which $x$ converges under $f^{(n_k)}(x)$ as $k$ goes to infinity, given the existence of a sequence $\{n_k\}$ such that $n_k$ goes to infinity as $k$ goes to infinity. A Milnor attractor is defined as a set $B$ satisfying the following two conditions.

1. $\mu(\rho(B)) > 0$, where $\mu$ is a measure that is equivalent to Lebesgue measure.

2. There is no proper closed subset $B' \subset B$ such that $\mu(\rho(B) \backslash \rho(B')) = 0$.

A Milnor attractor can be connected to unstable orbits that are repelled from the attractor. This situation in Milnor attractor differs from geometric attractors. A Milnor attractor may thus provide a mechanism for allowing both transitions from a state and returns to the state, which forms elemental behavior of what we have described as CI. This is the reason why we are interested in the study of this type of attractor.

### 3.2 Possible mechanisms of chaotic itinerancy

Let us discuss possible mechanisms of CI. It will be fruitful to discuss those with a kind of symmetry.

(1) *The case of symmetric systems*

(a) *3-tuple* (*Chaotic invariant set, Milnor attractors, riddled basins*)

Let $f$ be a differentiable map, which acts on the phase space $M$, $f : M \to M$. Let $q$ be a certain group action which acts on $M$ onto itself, $q : M \to M$. Now we assume that the dynamical system commutes with the group action, that is, $fq = qf$. Let $S(q)$ be the invariant set under the action $q$, that is, $S(q) = \{x|qx = x, x \in M\}$. Now take $x$ from such an invariant set $S(q)$. By $qx = x$, $f(qx) = f(x)$ holds. By the commutation assumption, $q(fx) = f(qx)$, and hence $q(fx) = f(x)$. The last equation means that $f(x)$ is also invariant, that is, $f(x) \in S(q)$. In other words, $S(q)$ is also an invariant set under the dynamics $f$. It is useful to find an invariant set for the dynamics, becasue while it is not necessary to find directly an invariant set under the dynamics, it is sufficient to simply find invariant set under a group action. The latter is much easier to perform than the former.

Let us consider a globally coupled chaotic map as a simple but typical example of this kind of symmetric system.

$$x_{n+1}^{(i)} = (1-\epsilon) f(x_n^{(i)}) + \frac{\epsilon}{N-1} \sum_{j \neq i} f(x_n^{(j)}), \tag{7}$$

where $n$ is a discrete time step, $i$ a discrete space indicating the position of each individual map on the space, $N$ the total number of maps, and each map $f$ is defined on the interval $I$. As a typical example, a chaotic logistic map is used, $f(x) = ax(1-x)$, where $a$ is fixed to produce chaos. All individual dynamics are assumed to be identical. Let us take a permutation of maps on a discrete space as a group action $q$. It is easily verified that the commutation assumption holds. For, evolving the dynamics $f$ for some fixed time $T$ after a certain permutation $q$ of the maps on a discrete space is equivalent to permuting the maps by $q$ after evolving the dynamics $f$ for $T$-time steps.

The simplest invariant set in this model is the synchronized state of all elements, $z_n$. Inserting $z_n$ into all $x_n^{(i)}$, i.e., $x_n^{(i)} = z_n$ in the above model equation (7), we obtain $z_{n+1} = f(z_n)$, which is, by definition, chaotic. Hence, we have a chaotic invariant set. There are many other synchronized states which are more complex than this basic synchronization, which was defined as partially synchronized state [19]. Partially synchronized state indicates, for instance, a combination of synchronized $N_1$ oscillators and another synchronized $N - N_1$ oscillators, where $N$ is the system size. These partially synchronized states can be an attractor. In this situation, if the Lyapunov exponent in the transversal direction to the chaotic invariant set is positive, the basins of such attractors have a topologically simple structure. However, if the transversal Lyapunov exponent becomes negative via a blowout bifurcation, then the flow toward the chaotic invariant set must exist with positive measure, on the one hand, and on the other hand, the flow toward attractors retains its positive measure. This situation produces a riddled basin structure and the appearance of curious transitory dynamics between the attractors with intervening chaotic trajectories. It should be noted that the attractors and also the chaotic invariant set are Milnor attractors. In this respect, one of the mechanisms of CI in the symmetric case is provided by the presence of the 3-tuple of chaotic invariant set, Milnor attractors and riddled basins, when an invariant set produced by symmetry is chaotic. However, the situation that chaotic invariant set cannot form the basis of the transition may appear. In such a case, it does not seem to be easy to permit chaotic orbits to appear between Milnor attractors. Furthermore, there cannot be a distribution of finite-time Lyapunov exponent in a transversal direction to a fixed point or a periodic point, whereas it is possible for a chaotic invariant set [30] and perhaps also for a torus, to exist.

Actually, we recently confirmed this matter by constructing a dynamic model [31]. The elementary dynamical system was made to possess a Milnor attractor of the fixed point as a basic invariant set. The $N$-coupled system with nearest neighbor interaction on a circle was considered. The transition of the CI did not occur from the point Milnor attractors, but occurred as a chaotic transition between tori. Here, a torus is produced by the interaction of point Milnor attractors.

(b) *The possibility of the connection between homoclinic chaos and Milnor attractors*

Under a similar symmetry, the saddle connections that are structurally unstable in conventional dynamical systems can be structurally stabilized as Guckenheimer and Holmes [51] have proved. For simplicity, we consider the case of a saddle connection between two saddles. Let us call them $S_1$ and $S_2$. The condition of stabilization for the connection from $S_1$ to $S_2$ is that the sum of the dimensions of the unstable manifold of $S_1$ and the stable manifold of $S_2$ exceeds the dimension of the space. The symmetric dynamical system consists of invariant subspaces. In each subspace, we can confirm this condition.

However, with only this kind of stabilization mechanism, *chaotic* transitions cannot be proved. What is a mechanism for allowing chaotic transitions, based on the saddle connections? Suppose $S_2$ changes its stability in unstable directions to produce neutral stability. In other words, the saddle $S_2$ is supposed to change to become a Milnor attractor, $S_{m2}$. In these neutral directions, the orbits move away from such a Milnor attractor. Those orbits may make a heteroclinic orbit connecting to $S_1$, but this should be structurally unstable for the following reason. The fact that the sum of the dimension $n_1^u$ of the unstable manifold of $S_1$ and the dimension $n_2^s$ of the stable manifold of $S_{m2}$ exceeds the space dimension $N$, that is, $n_1^u + n_2^s > N$, indicates $(N - n_1^u) + (N - n_2^s) < N$. The last inequality means that the sum of the dimensions of the stable manifold of $S_1$ and of the unstable manifold of $S_{m2}$ cannot exceed the space dimension. In other words, the intersection of the two manifolds makes only a measure-zero set in the phase space. Thus, heteroclinic chaos must be expected in a neighborhood of $S_1$, as in the Shilnikov type of bifurcation. Chaotic itinerancy may occur among the Milnor attractors via chaotic orbits if more saddles exist originaly. This scenario might explain the chaotic switch between synchronized and desynchronized states observed in several networks of class I neurons, which will be discussed in the last section.

(2) *The case of asymmetric systems*

What can we state in the case without symmetry? If we start with the symmetric systems and then perturb them to lose that symmetry, then we will find a quite similar situation to the symmetric case. Actually, asymmetric connections in a GCM, which is obtained by the perturbation of a conventional GCM, produce similar characteristics to CI in the symmetric case. The nonequilibrium neural network model for successive association of memories, which is one of the pioneering models of CI, however, lacks the smooth continuation of the symmetric systems. Although the chaotic transition between fixed point attractors in Milnor's sense requires a little noise, the role of noise in this case seems to be different from the symmetric case, because we did not find a riddled basin structure for each memory state. Hence, the mechanism of CI in the asymmetric case of this type might be different from the symmetric case. No clear theory has, however, so far been proposed, although several concepts have been investigated to discover its mechanism. At least three cases can be considered.

(a) *Are saddle connections possible?*

Because symmetry is lost, the space to be considered is a whole phase space, not an invariant subspace. Now consider two saddles connecting with each other. As discussed above, when the saddle connection cannot be stabilized, chaos appears. This consequence can be extended to the cyclic connections of $m$ saddles, that is, such connections are not structurally stable, and hence chaos will ensure. However, this situation seems to lose stagnant motions such that the orbits stay at attractor ruins or near Milnor attractors over a long time.

(b) *Genesis of heteroclinic tangency within a chaotic invariant set*

Heteroclinic tangency may bring about a neutral situation, and hence its appearance may give rise to the degeneracy of zero-Lyapunov exponents if such tangency becomes dominant, compared with transversality. Stagnant motions are expected in a neighborhood of such tangency. This case must be studied in details.

(c) *Milnor attractors associated with fractal basin boundaries*

This is a highly hypothetical situation. It is known that fractal basin boundaries separates multiple attractors [52]. With respect to CI, Feudel et al. found a CI-like phenomenon in the double rotor system with small amplitude noise [52]. In this system, many periodic orbits coexist, with the higher periodic orbits possessing very tiny basins which disappear under the influence of noise, leaving only the low periodic orbits. A similar situation to this was found in the KIII model by Kozma and Freeman [28], where because of fractal basin boundaries, long chaotic transients appear before the system falls into a periodic orbit. Orbits are trapped for some time in the vicinity of periodic attractors, but eventually are kicked by noise into the fractal boundary region, where the orbits become chaotic again, and consequently repeat the transitions between chaotic and periodic attractors. This is a noise-induced CI-like phenomenon. We must consider for the deterministic case: how could such attractors become a Milnor attractor? This is still an open question.

## 4 A neuron-assembly model for transitory dynamics of synchronization

In relation to neurocomputing, CI was found in many neural systems such as nonequilibrium neural networks for successive recall of memories, the neural network model for regenerating episodic memory [53, 54], the dynamic associative memory model [44, 21, 55], the modified Hopfield model for the travelling salesman problem [56], and the partially connected network for associative memory [57]. The concept of CI has been adopted to provide a dynamic interpretation for the processes of perception and identification [11–13, 16, 28]. These processes in animal and human behavior are often observed, accompanied by gamma-range oscillations.

On the other hand, model studies on the dynamics of the class I neuron and its network have recently been highlighted, in accordance with the accumulated experimental data on various ion-channels. Furthermore, experimental evidence has also accumulated on the ubiquity of gap junction couplings in a large number of invertebrate brains and also in the mammalian neocortices. The origin of gamma-range activity in neuron assemblies has also focused, in particular, on the discovery of gap junction networks and their chemical-synaptic interactions with principal cells like pyramidal cells.

An irregular change between synchronization and desynchronization was also studied by using the Morris-Lecar model [58]. Whether or not this irregularity stems from chaos has not been studied. Moreover, it is known that this irregular alteration of synchronized and desynchronized states only occurs in a very narrow parameter region. An irregular and seemingly nonstationary alteration between synchronized and desynchronized states has actually been observed in animal experiments [12–14, 17], although the observed activity level differs in each experiment. This level difference may represent the difference of meaning of synchronization.

Physiologically, the functions of class II neurons are characterized by $Na$- and $K$-ion channels such as those described by the Hodgkin-Huxley equations, whereas the function of class I neurons is further determined, typically by the transient, slowly inactivating $A$- channels in addition to the $Na$- and $K$- channels. From a mathematical point of view, this functional difference can be reduced to and represented by the different type of bifurcations.

The phase space of a class II neuron, which is defined by the voltage of membrane potential, and the levels of activity and inactivity in ion channels, is characterized by a distorted vector field, thereby the large excursions of electric activity indicating the production of a transient spike. The repetitive firings of spikes are represented by a sustained oscillation of a limit cycle oscillator, which is produced via Hopf bifurcation. The limit cycle starts as an infinitesimal amplitude in the case of supercritical Hopf bifurcation, while on the other hand, in the case of subcritical Hopf bifurcation, it starts from a finite amplitude. In both cases, it preserves almost the same frequency over a relatively wide range of bifurcation parameters, such as the input current. For a large deviation of the bifurcation parameter from the bifurcation point, the frequency simply depends linearly on the amplitude of the deviation.

The class I neuron is characterized by the interplay of a saddle-node bifurcation with a Hopf bifurcation. Because of the presence of a saddle-node bifurcation, the frequency of the limit cycle oscillator produced by the Hop bifurcation is changed markedly by a slight change of the bifurcation parameter, such as the input current. In other words, the dynamic range of the response becomes extremely large because of the presence of the saddle. Various mathematical treatments of the similarities and differences of both class I and II neurons and of their models have been recently systematically reviewed [59].

We summarize below the chaotic behaviors obtained in published mathematical models of networks of class I neurons with the gap junction. Here the gap junction couplings can be modeled by diffusion type couplings.

(1) Nearest neighbor couplings with gap junctions of Connor-type neurons: there are no reports relating to chaotic behavior.

(2) All-to-all couplings with gap junctions of Morris-Lecar-type neurons: the chaotic alteration of synchronized and desynchronized states over a very narrow parameter region was observed [58].

Recently, we investigated [62] the dynamic behavior of the network consisting of the nearest neighbor couplings with gap junctions of Morris-Lecar-type neurons. We observed chaos over a very narrow parameter region. There have not been any observations so far of chaotic alteration between synchronized and desynchronized states.

We have, then, proposed a model of the cell assembly of a subclass, class I*, of class I neurons with gap junction-type of couplings, as deduced from the Rose-Hindmarsh model [60]. It was found that the spatio-temporal chaotic behavior is a typical dynamic behavior in the gap junction-coupled class I neurons, whereas pulse propagation as well as spiral wave propagation is typical of gap junction-coupled class II neurons [61, 62]. More details can be found in the article [63]. We have also proposed a simple neuron model with two variables, designed to possess both bifurcations mentioned above. This model, called the $\mu$- model, is similar to the reduced model of Hindmarsh and Rose [64]. We found a chaotic transition between synchronized and desynchronized states in the gap junction-coupled $\mu$-model that has similar symmetry to the one mentioned above, that is, the whole synchronized state constitutes an invariant subspace. Based on numerical studies, we have further proposed a hypothesis that this transition can be described as CI. We are now investigating the mathematical mechanism of this chaotic transition, which will be published elsewhere.

## 5 Summary and discussion

We have reviewed the concept of chaotic itinerancy and several models of chaotic itinerancy including the models of neural systems. We have also reviewed the possibility of information processing with chaos and chaotic itinerancy, based on the information theory of chaos. We have further discussed possible mechanisms of chaotic itinerancy, although there are still several ambiguities that require resolution.

We have finally introduced the most recent study on chaotic itinerancy. This study investigates building a new framework for the mathematical modeling of neural activity, based on the experimental findings of functional organization at the mesoscopic activity level of cell assemblies. We found that a simple model neural system consisting of class I* neurons with gap junction-type couplings has transitory dynamics similar to chaotic switching between synchronized and desynchronized states as observed in several biological neural systems.

There are varieties of desynchronized states including local metachronal waves which are a weakly unstable form of partial synchronization. It is worth investigating whether or not the synchronized state can be described by a Milnor attractor. Related to this, it will also be worth studying how metachronal waves can act to destabilize the synchronized state. Although this neural system has a symmetry, it does not seem to be possible to produce a riddled basin. Therefore, another scenario must be considered for the presence of CI in this system. Further studies are necessary to clarify the mechanism of the chaotic change of synchronization.

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